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MASTER IN BIOLOGY OF ORGANISMS AND ECOLOGY

Grouse species as a conservation tool: effects of habitat dynamics on distribution and abundance of the black grouse (*Tetrao tetrix*)

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FACULTES UNIVERSITAIRES NOTRE-DAME DE LA PAIX
NAMUR

Faculté des Sciences

**GROUSE SPECIES AS A CONSERVATION TOOL - EFFETS OF
HABITAT DYNAMICS ON DISTRIBUTION AND ABUNDANCE OF
THE BLACK GROUSE (*Tetrao tetrix*)**

**Mémoire présenté pour l'obtention du grade de
licencié en Sciences biologiques**

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Grouse species as a conservation tool – effects of habitat dynamics on distribution and abundance of the black grouse (*Tetrao tetrix*)

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Résumé

La gestion et la conservation de la biodiversité devraient idéalement prendre en considération toutes les composantes de la biodiversité, i.e. les espèces, les habitats, les gènes et les fonctions des écosystèmes, à différentes échelles s'étendant d'un simple arbre à l'unité de gestion forestière et jusqu'aux paysages, au niveau des régions. A chaque échelle, différents acteurs sont impliqués. Etant facile à communiquer, la composante « espèce » de la biodiversité est donc d'un intérêt particulier. Ceci a mené au concept d'espèces « parapluie » qui devraient être les espèces les plus spécifiques et les plus exigeantes au niveau de la surface, pour chaque type d'environnement.

Les forêts boréales sont caractérisées par leur dynamique : elles sont dominées par une distribution morcelée de différents stades successifs dans la forêt. Les forêts boréales suédoises fournissent donc une bonne opportunité d'étudier si et comment les populations animales répondent à ce morcellement : elles peuvent être utilisées comme référence pour l'élaboration des objectifs de conservation dans les régions où une réhabilitation de l'habitat est nécessaire pour maintenir la biodiversité.

Cette thèse est divisée en trois parties. La première est une vue d'ensemble des facteurs affectant la distribution et l'abondance des populations de tétras-lyre (*Tetrao tetrix*). La tendance générale au déclin en Europe est en grande partie attribuée à la perte d'habitat. Il faut néanmoins garder à l'esprit le fait que, à un niveau local, l'importance relative des différents facteurs est très variable. Donc, chaque population devrait bénéficier d'un plan de gestion propre. Dans la deuxième partie de cette thèse, l'évolution de la luminosité au sein des forêts boréales a été étudiée, depuis le stade coupe à blanc jusqu'aux forêts centenaires. Ceci, parallèlement à l'évolution de la couverture végétale au sol. Il apparaît que la « fenêtre » dans le temps utilisée par le Tétras lyre (jeunes forêts: 6-25 ans) est caractérisée par un important couvert végétal entre 1.3 et 4 m au-dessus du niveau du sol, ainsi qu'une proportion importante de bruyère (*Calluna vulgaris*) dans le couvert végétal. Quant à la troisième partie, il s'agit d'une étude à long terme, corrélant la dynamique de populations locales de Tétras lyre à la dynamique de leur habitat. Ce travail a été réalisé au sein d'un transect dans la forêt boréale suédoise caractérisé par trois sous-régions. Celles-ci se différencient par le type d'habitat dominant : jeunes forêts, grands marais ou habitat disparu. Lorsque l'habitat est majoritairement constitué de jeunes forêts, très dynamiques dans le temps, les populations de

Tétras lyre se déplacent afin de « suivre » leur habitat. Par contre, lorsque l'habitat est stable, tel les marais et les tourbières, les populations sont spatialement fixes. Enfin, cette troisième partie a été resituée dans un contexte européen, en comparant l'évolution et la dynamique de populations locales en Europe aux trois sous-régions du transect. A nouveau, il ressort que à habitat dynamique correspond une population dynamique et vice-versa.

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Introduction - biodiversity conservation at the landscape scale

At the beginning of the 3rd millennium, biodiversity conservation has become a major challenge to society.

Biodiversity is usually used to describe the number, the variety and the variability of living organisms. This includes the genetic variability within species and their populations, the variability of species and their forms of life, the diversity of associated species complexes within habitats and ecosystems; from the genes to the landscape (Dufrêne, 1997). Additionally, different ecosystem processes are included.

The first step in its conservation is to assess the total biodiversity that one should find in a natural or otherwise authentic landscape. In Europe this is a difficult task as almost all natural environments have disappeared and are managed. This means that references are hard to find. However, it is important to have benchmarks against which biodiversity measurements can be compared; mainly because time lags in the response of species populations to habitat loss may overestimate the viability of species. The time period during which a species persists after habitat destruction is called the time delay. Theoretical considerations show that the time delay is greatest for species for which the degraded environment is near the threshold for persistence. The number of species that are expected to become extinct due to past adverse environmental changes is called extinction debt (Hanski 2000). In the case of black grouse in Europe, the boreal forests can be used as benchmarks because in these forests the black grouse populations are viable. The second step in the conservation of biodiversity is to define the minimum size of habitat requirements for the different species. As this is impossible to realize for all species, different types of surrogate species are used in conservation planning, with umbrella species appearing as particularly interesting as tool for biodiversity managers. Umbrella species are species whose conservation confers a protective umbrella to numerous co-occurring species because they are the most specialised and demanding ones of each forest environment/biotic process (see Simberloff 1998; Caro and Doherty 1999). Ideally, the suite of umbrella species should cover all types of forest environment and the different spatial scales from trees to landscapes.

Once this has been done and the quantitative knowledge about the habitat requirements of the species are known, managers have to analyse the gaps in the amount of habitat that is needed for long-term biodiversity conservation and the suitable available habitat. This will eventually show how much of each habitat needs to be restored and/or recreated (Angelstam and Andersson 2001).

Grouse as conservation tools and potential umbrella species

As specialists with fairly narrow habitat needs but large spatial requirements, grouse are well suited for studies of wildlife-habitat relationships and landscape ecology (Angelstam et al. 2000).

As a result of their sensitivity, grouse have often been considered to be indicators of the health of the ecosystems they inhabit. The presence of an indicator species is believed to indicate suitable habitats for other species as well (Landres *et al.* 1988). For example, Fisher (1999) and Graf (1998) concluded that their results support the use of capercaillie (*Tetrao urogallus*) as an indicator of ecosystem health and biodiversity in managed alpine forests. Conservation efforts to preserve grouse habitat are thus likely to benefit other species associated with the same habitat.

Moreover, its attractiveness to people makes black grouse a suitable flagship species to promote the conservation of biodiversity, especially in central and western Europe. This bird is hence a potential "umbrella" for other species with similar habitat affinities but less area requirements (Angelstam 2001).

Umbrella species should of course been well-known by scientists. The aim of this thesis is to relate the habitat dynamic to the population density and dynamics of black grouse in different characteristic European habitats. This thesis has three parts. First I review the habitat and other factors that affect black grouse at the level of individuals, populations and meta-populations. Then I present the results from a field study about the temporal dynamics of vegetation structure and food plants after clear-cutting in boreal forest. Finally, I report a study on the effects of 23 years of landscape dynamics on the distribution and abundance on the black grouse. The results of the field studies are discussed in the context of black grouse conservation in Europe.

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Chapter 1 - A review of the factors affecting the distribution and abundance on the black grouse

When discussing land management and the maintenance of biodiversity, the imperative importance of considerations at multiple spatial scales must be kept in mind. For the maintenance of long-term viability of species, three hierarchical levels can be distinguished. First there is the individual level, which relates to the day-to-day requirements of a single individual, a breeding pair or other social unit. Second, there is the population, i.e. all the individuals in a landscape at a given time. Finally, the range of a species can be divided into different metapopulations. A metapopulation encompasses distinct populations, which have no or few interbreeding, thus characterised by different pools of genes.

From a management point-of-view this means that different management actors will be able to work at a restricted set of spatial scales. With the black grouse as an example, a single small landowner can usually affect this species at the individual level only. Consequently the management of populations requires a well-integrated work of small private landowners, large companies, villages and even regional planners. For an area-demanding species as the black grouse, the metapopulation scale would require international co-operation.

In the following these three levels within the range of a species are used to stratify the different factors that affect black grouse conservation in Europe. We here review the factors causing the decline in black grouse populations. They are classified with regard to the level of management, which should take them into account. For each of them, I propose variables that could be measured by managers to quantify their importance.

Individual level

a) Black grouse habitat

Species usually require different biotopes (i.e. land cover types being affected by a combination of abiotic, natural and anthropogenic biotic factors) during the course of the annual cycle, and sometimes also during its life cycle. To be defined as the species habitat, an area must contain all those needed biotopes.

Throughout its range, black grouse is found in open to semi-open vegetation types that range from natural moors and bogs, young several stages in the forest succession to old cultural landscapes.

Young successional stages in forest after stand-replacing disturbances

In the boreal forest, black grouse prefer seedling and young stands, while fresh clear-cuts and older forests are generally avoided (Börset et al. 1973, Marcström et al. 1982, Angelstam 1983). Today, in managed boreal forest landscapes, clear felling almost exclusively creates this habitat type. Such patches usually become inhabited within five years after logging and last for 25 up to 35-40 years depending on the productivity of the forest, being high in the southern parts of Sweden but low in the north (Angelstam 1983). As patches become unsuitable, local populations go extinct, while other local populations are established as new patches arise.

The open bog

Raised bogs and bog/fen complexes constitute natural black grouse habitats. Their quality is largely constant relative to the anthropogenically changing surrounding habitat types (Bergmann and Klaus 1994), and may last for hundreds of years. Among several types of bogs and mires described by Byrkjedal et al. (1997), the open sparsely vegetated ones are preferred.

During the last decades several mires and bogs in Western Europe have been exposed to airborne nitrogen, which acts as a fertiliser, and this has caused a succession of Scots pine and deciduous shrubs (Ellenberg et al. 1989). As a consequence, the encroachment of shrubs is gradually changing the bogs from an open habitat type to a forest, which is not suitable for the black grouse.

The most serious threats to the mires and bogs, listed in order of importance in European areas by Byrkjedal et al. (1997) are: afforestation, peat extraction, tourism, other agricultural improvement, pollution (i.e. nitrogen deposition and acid rain).

Habitat types of the old cultural landscape

- Meadows

Few terms have been as confusing and misused as the concept of meadows (Ihse 1997). While cultural historians usually focus on man and his traditional management of habitats and landscapes, botanists focus on plant species, plant communities and biotic factors. Here, the old cultural landscape aspect is adopted and the meadows are viewed as usually permanent grasslands, traditionally maintained by the cutting of hay often combined with the lopping or pollarding of deciduous trees, which were commonly present in the meadow (Bergendorff et al. 1996). The tree species used as cattle winter fodder were mainly *Betula*, *Carpinus*, *Fagus*, *Fraxinus*, *Tilia* and *Ulmus* (e.g. Slotte 2000). In the absence of draining and amalgamation of fields, shrubs and bushes are common. The resulting habitat structure is an open to semi-open woodland.

Since this habitat type is barely present anymore in Sweden, a look at historical situations or countries still using old methods of agricultural management is necessary. Such a situation is still found in parts of the Alps (Glutz et al. 1973) and areas where the old cultural landscape has been maintained (e.g. Waldviertel in N Austria and Rhön in Germany, Schmaltzer A. and Kolb K.-H., pers. comm.).

The presence of black grouse populations in old cultural landscapes was a result of the anthropogenic mosaic of different habitats such as fields and meadows lined with various habitats suitable for retreat, breeding and winter foraging (Klaus et al. 1990, Kolb 1996, Schmaltzer A., pers. comm.). In the Åland archipelago in the Baltic, where the cutting of hay in meadows was practiced quite recently, the population size of black grouse declined along with the cessation of the traditional management of wooded grasslands, and the subsequent re-growth of trees (Slotte 2000). According to Haila et al. (1980), the Åland black grouse population declined by 80 % since the 1940s, attributed to afforestation of open, grazed heath and small agricultural field and forest mosaics. Similarly, Scherzinger (1976) argued that the

cultural landscape satisfies the requirements of the black grouse habitat. As an example he mentioned that leks often are situated in large patches of heaths, pastures and meadows.

- Pastures and forest grazing

While the meadows often were placed in connection to the farm, the pasture evolved in the peripheral land, or as a result of grazing in former meadows (Ihse 1997). Along with the change in forest structure by woodland pasturing, the dense forests gradually were converted to a more open forest with openings and glades in the forest (Berglund et al. 1991, Almquist-Jacobson 1994, Lagerås 1996, Skånes 1996, Nilsson 1997, Björse 2000). In open forests, more light reached the ground, which gave higher insect abundance (Hansson 1983), thus providing an important feeding habitat to the newly hatched chickens. Historically, the forests provided pasture and fodder for a range of livestock for a long time. In all European countries, however, the general trend over the last four decades has been to abandon such pastures (Tucker and Heath 1994).

The old literature supports the idea that the old cultural landscape with pastureland and the edges between forest and pasture were important habitats (Andersén 1861, Anonymous 1865, Anonymous 1881, Anonymous 1883, Sjögrén 1885, Ekström 1894). In the dark coniferous forest these birds were never found.

- Lowland Atlantic heathland

Rebane and Wynde (1997) defined lowland Atlantic heathland as an open, mainly treeless habitat dominated by dwarf shrubs of the heath family (*Ericaceae*), usually heather *Calluna vulgaris*, or other species of similar appearance. Heathland gradually evolved through forest clearance and subsequent grazing (Schager 1909), as an effect of increasing needs of grazing habitat for domestic animals, as the human population grew. In southern Sweden, the heaths were maintained by a combination of grazing and turf cutting. This ancient agricultural system was practiced for around 1000 years until it ceased in the twentieth century (Damman 1957, Malmer 1965).

- Alpine meadows and lowered treeline

In the Alps, an open forest structure as well as ground vegetation with dwarf shrubs such as *Vaccinium* and *Rhododendron* are important for the black grouse. The tree species composition is not important for the occurrence of the black grouse. In the Northern Alps, subalpine spruce forests are used as habitat, in the Central Alps black grouse occurs in larch-stone pine forests as well as at and above the treeline. So-called larch meadows (open larch forests that are used as pasture) comprise habitat in the Southern Alps, as well as alder stands or even beech forests which often can build the tree line, historically lowered by human activity (Klaus et al. 1990). The species distribution range is most often located at the northern and north-eastern slopes as it is there where snow conditions remain soft the longest and, during the winter, black grouse rest in the cover of snow tunnels.

⇒ The summed amount of the three main black grouse habitats: bogs, young forest stand, old cultural landscapes (sq. km) provides a measurement of the total amount of potential habitat.

b) Patch size and landscape grain

As a habitat specialist, the black grouse density 'tracks' the amount of its habitat within a landscape. However, birds have a minimum area requirement: the size of the habitat patch has to be sufficiently large, usually in the order of 100 ha for a lek (Angelstam 1983). This relation can also be used in the opposite direction. With knowledge about the amount and patch size distribution of the habitat in a landscape, the black grouse density should be predictable. The land cover proportion in a landscape can thus be divided into the following categories

	Patch size requirements not satisfied	Above patch size requirement satisfied
Habitat		
Not habitat		

Consequently a very fine-grained landscape (many small patches) will be unsuitable to the black grouse even if the total amount of biotopes is large.

The range of patch sizes and/or the medium patch size is thus a second step for whom making nature management. Only the patches with the required minimum area will be taken in account to calculate the amount of habitat.

⇒ Suitable measurements are the range of patch sizes and the medium patch size.

Consequently, the number of owner of a determined area is also important when speaking about patch size.



Figure 1: This figure represents the "graininess" affecting suitable habitat for black grouse, depending on the number of owners of the area.

If few companies each own big areas, the patch size in which trees are of the same age will be bigger than if the land is owned by small private land owners. In this case, even for the same proportion of suitable stands is the same, the 'graininess' could be too fine. As a result, species could be unable to leave in the second land structure.

⇒ Number of owners or medium size of properties (sq. km).

c) Grazing and browsing

Intensive grazing by livestock, deer or other wild ungulates can significantly affect the structure, height, and species composition of vegetation and thus destroy or degrade cover, nesting, and feeding habitats of grouse (e.g. Baines 1996).

Grazing regimes may affect breeding success of black grouse in three main ways. First, high levels of grazing can reduce the abundance of key food plants in early spring (Angelstam et

al. 1984; Hudson 1992) which may lower maternal condition prior the breeding (Drent and Daan 1980). Secondly, better cover for nests and broods may reduce the effect of predators. The role of predators in reducing densities and breeding success has been demonstrated in several experimental studies of tetraonids (Lindstrom et al. 1987; Marcstrom, Kenward and Engren 1988). Thirdly, chick survival in several species of game birds correlates with the abundance of preferred insects (Green 1984; Hill 1985). According to Kaasa (1959), moth caterpillars (Lepidoptera), sawfly (Symphyta) and ants (Formicidae) are the preferred prey of black grouse chicks. In these studies, low numbers of invertebrates were inversely correlated with distances moved by broods of partridges and pheasants. Large daily movements by foraging broods prove costly and are associated with poor chick survival (Baines 1996).

However, a moderate level of livestock grazing can be compatible with grouse populations. In some instances, livestock herding has even improved grouse habitat, e.g. in the Alps, where large-scale pasturing of cattle and sheep has significantly increased the area suitable for black grouse in lowering the tree line.

- ⇒ Density of grazing/browsing mammals (wild ungulates/livestock)
- ⇒ Density of preferred insects (moth caterpillars, sawfly larvae and ants)

d) Effect of forestry on winter habitat quality: a measure of the naturalness

The effect of the changes in the forest composition is potentially important in winter. In summer, field layer plants and shrubs form the basic food of black grouse. However, when the snow covers the ground, the feeding is made in the tree stratum. Birches (*Betula sp.*) are especially used in North and Central Europe while, in the Alps, coniferous trees are also consumed (*Juniperus sp.*, *Picea abies*, *Pinus sp.*, *Sorbus aucuparius*, *Alnus sp.*). According to Klaus (1991), in spruce dominated forests on the crests of the Central European mountains and in the Northern Alps, birch and/or rowan are often the limiting factors for black grouse and capercaillie (*Tetrao urogallus*) in winters with deep snow. Consequently, where the snow depth is large, black grouse could be negatively affected by intensive forest management that will remove the possibility of feeding on trees.

The differences between natural forests and those managed by forestry are most marked in the middle-aged forests: forestry limits the proportion of deciduous trees by removing them and by planting spruces. The final stages are more alike, since coniferous trees occupy the dominant position in the later seral stages in natural conditions also, and deciduous trees disappear (Seiskari 1962).

- ⇒ Percentage of deciduous trees (or birches) within the forest

Population level

a) Patch density

The species habitat within a landscape is the “summed amount of suitable habitat” which patches are superior/equal to the minimum required area.

- ⇒ A suitable indicator is the proportion of patches offering minimum required area

b) Patch dynamics

The duration of different biotopes varies. Bogs are stable over time but during the last decades several mires and bogs in Western Europe have evolved into forest because of nitrogen fertilisation. Others are drained to meet the increased needs for agricultural land. Old cultural landscape is stable as long as it is managed, but goes extinct if not managed. This traditional agriculture, characterised by extensive farming methods has decreased in Western Europe. However, such a situation is still found in parts of the Alps (Angelstam 1983). Young forests are ephemeral; they appear or after large stand-replacing natural disturbances or after clear-cutting. As trees are growing, ground vegetation will evolve with the light reaching the soil. It constitutes a suitable habitat for black grouse from 5 to 25-30 years after the disturbance event. Young forests are very dynamic and can be viewed as patches which “move” in the landscape.

⇒ Regarding to the dynamic of the landscape, managers can calculate the area to be protected or to manage.

c) Fragmentation affects predation rates

The land cover composition may also have indirect effects on black grouse. Even if several patches are big enough to support a population, its survival can be a failure because of fragmentation which has consequences on biotic interactions with the surrounding matrix. In the case of black grouse, several studies have pointed out that landscape fragmentation results in an increased predation pressure. Kurki et al. (2000) found a positive relationship between habitat fragmentation and generalist predators favored by an agricultural matrix providing suitable food for them. For example, voles (*Microtinus*) are favoured in grass-rich habitats, i.e. clear-cuttings and plantations, this mean that their predator density will also arise and have a further impact on the nests and young of ground-nesting species like black grouse.

Also in this case, the spatial scale is important. At the landscape scale, the probability to see a hen with a brood decreased with the proportion of agricultural land. However, on a smaller scale, hens with a brood were more likely to be found in near agricultural patches than those without a brood. Actually, agricultural lands are not distributed at random. They are mostly found on areas with high natural productivity; thus, the productivity and structure of the surrounding forest stands may also differ, providing a better brooding habitat for grouse (Kurki et al., 2000).

Nests are distributed in all habitat types, whereas broods are restricted to specific brood habitats (insect-rich forest types in late seral stages). This is why the predator gain of searching for nests is independent of forest fragmentation. However, the gain of searching for broods increases rapidly when suitable brood habitat is reduced to 20-30 % (Storaas *et al.* 2000). Kurki and Linden (1995) also pointed out that the brood size was not affected by landscape composition, thus, predation pressure in fragmented landscapes causes total losses of either nests or broods.

- ⇒ Proportion agricultural land/forest
- ⇒ Density of road network
- ⇒ Distance between leks (km)

d) Hunting and poaching

Where black grouse hunting is still permitted, the best period for reducing the population impact is the autumn. Because at that time, many birds in the hunting bag will be juveniles

(some of these probably would not have survived the winter). By contrary in spring, the population is at its smallest size and birds shot are potential breeders (Ellison 1991).

However, it should also be noticed that if hunting of any kind is banned, a major interest group, hunters, may loose interest in habitat management.

- ⇒ Bag records or estimation of the poaching pressure
- ⇒ Estimation of poaching pressure (+/0)

e) Human disturbance

Human disturbance, like the development of roads, ski-stations and tourism does not have large scale impacts unlike agriculture and forestry. Nevertheless, where populations are already endangered, it could cause significant mortality: collision with power-lines, deer fences (Beveranger 1995; Baines and Summers 1997; Miquet 1996).

It has also been shown that even if the habitat is suitable for grouse, too frequently outdoor human activities can make it abandoned by grouse. The escape of a grouse flushed by a skier is energy-consuming and may expose the bird to predators, and reduces the time available for foraging. If disturbed repeatedly, death from starvation or predation is a likely consequence. Frequent presence of humans may expel animals from otherwise optimal habitats - the result equals habitat loss and fragmentation (Storch, 2000). Tourism can also have an impact on the distance between leks: if cocks are too disturbed in a place, they will move to another one. This may perturb other leks as becoming too close of those later. Domestic animals can also be a source of disturbance, which is “human-linked”.

- ⇒ Estimation of the tourism pressure (+/0)

f) Population density

Small populations are generally vulnerable and show a high risk of extinction due to chance environmental or demographic events. A series of years with unsuitable weather or the loss of a few females to a predator can be enough to extirpate a small population. Most grouse populations may fluctuate greatly in relation to annual weather conditions and other environmental factors. Therefore, an isolated grouse population should probably number at least several hundred birds in order to have good (>90%) long-term (100 years) survival chances (Storch 1995).

- ⇒ Number of black grouse in the population
- ⇒ Number of lek / unit area (100 sq. km)

g) Management

In areas where management occurs, it should be interesting to get several information about it, to see if it effectively has an impact on the maintaining of black grouse population.

- ⇒ Type of management
- ⇒ Number of years of management
- ⇒ Intensity of management (+/0)

Metapopulation level

a) Population isolation

At the continental scale in Europe, grouse are restricted to isolated distribution ranges. Nearest neighbour distances average 54 km for black grouse whereas maximum reported dispersal distance is 34 km. This means that exchanges between most distribution ranges are unlikely (Storch 1997).

Many populations have less than 100 birds, which is most probably too small for long-term viability. Connectivity is ensured by dispersal. Thus, dispersal between local populations may be of major importance.

Juvenile birds disperse between local populations and thereby keep these populations alive, an effect called demographic rescue. Dispersal is also important to re-colonize vacant patches of habitat.

Therefore, conservationists concerned with remnant grouse populations also have to consider the potential donor populations. Conservation policy might be wrong in concentrating efforts exclusively on populations close to extinction (Storch 1997).

⇒ Distance between populations (km)

b) Predators

Black grouse is a ground nesting bird, thus it is quite vulnerable to nest predation. Its main predators are generalists, i.e. they don't only rely on black grouse: red fox, raven, crow (Klaus 1984).

Northern boreal populations are characterised by cyclicity in the breeding success. Some scientists tried to find any prey-predator relation but none succeeded. However, the "alternative prey" hypothesis is supported up by some of them. When vole density decreases, their main predator, foxes, will then shift their diet on black grouse (Angelstam et al. 1985). Cycles disappear towards the south. This can be explained by the highest predation pressure in southern regions related to a higher proportion of agricultural land (Kurki et al. 2000).

Actually, predation is only a problem for black grouse in regions where other disturbances already occur. In natural habitat they are quite capable to live together with their predators without any long-term negative impact on their population.

⇒ Density of black grouse predators (number of red foxes, corvids,...)

⇒ Estimation of the predation pressure (+/0)

⇒ or Bag records of predators

c) Climate

Some studies tried to model the climate influence on black grouse population dynamics (Loneux 1997). The results suggest that a hot and dry summer weather benefits to chicks during their first weeks. When the chicks are very young, they are not homeotherm yet; thus, if the weather is cold and rainy, they take refuge under their mother wings, i.e. they spend less time looking for food. Another consequence of such a weather is that arthropods are less abundant. If these weather conditions last too long, they will starve. Cold winters are more benefit to black grouse than mild ones. This confirms their adaptation to a boreal life: the hibernal metabolism is very reduced and they are adapted to long period of physiologic rest, if possible in the cover of snow tunnels. During cold weather, snow-roosting is crucial for those

birds, even little disturbances can have a great impact on their energetic balance. Different climate variables indicate:

- ⇒ Temperature trend (C)
- ⇒ Rain train (mm/month)
- ⇒ Medium snow height during winter (cm)
- ⇒ Number of days with snow

d) Pollution

Some kind of pollution, such as acid rain, may have impacts on the vegetation. Acid rain results in eutrophication and the vegetation changes could be negative for the black grouse. It can directly affect its quality but also the ice composition, which recover the food during winter (Marjakangas and Moss 1991).

- ⇒ Nitrogen content (impact: +/- no impact: 0)
- ⇒ Acid rain (impact: +/- no impact: 0)

e) Introduction of species

The introduction of new species is well known to disturb the ecosystem. In the case of black grouse, the introduction of *Phasianus colchicus*, by hunters, has a negative impact as they have nearly the same preferences (Reichholf 1982, in Bergmann and Klaus 1994).

- ⇒ Effect of introduced species (impact: +/- no impact: 0)
- ⇒ Density of *Phasianus*

Conclusion

When studying the effects of different factors on the distribution and abundance of species, the landscape scale is important. Some factors will affect only a local population whereas others will have landscape scale impacts. In the case of the black grouse, factors reported to affect its populations in Europe are numerous. However, habitat degradation and loss due to change in human land-use are generally perceived as the major causes of black grouse decline.

However, to understand the relative importance of different factors affecting the black grouse, we propose case studies in landscapes with different deviations from the reference areas with viable black grouse populations.

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Chapter 2 - Temporal changes in the abundance of habitat structure and important food plants for black grouse after removal of old boreal forest

Introduction

Natural boreal forest is subjected to several kinds of external natural disturbances such as fire, wind, avalanche (Bonan and Shugart 1992). This produces stands with several age-classes of trees. Nowadays such natural disturbances do not occur anymore. However, by clearcutting, humans to some extent emulate the natural dynamics of the boreal forest. Patches of young forest are continuously “formed”. However, biologically old successional stages are usually largely incompatible with forest management, as most of the time, trees are cut after 60 to 100 years (Angelstam and Andersson 2001).

Black grouse (*Tetrao tetrix*) prefer young forest stands: 5-25 years old (Seiskari 1962 and Swenson and Angelstam 1993). So when an old forest is removed by large-scale disturbances such as fire, storm, avalanche or by human impact such as clear-cut, it becomes a suitable habitat for black grouse.

The aim of this paper is to describe how the habitat structure and abundance of important food plants in boreal forest changes over time after the removal of old forest. We will then try to use the data to understand why black grouse only uses that "window" in time and avoids older forests.

Two hypotheses are tested. First, that the appropriate open woodland structure is restricted in the succession. Second, that the abundance of the food preferred by black grouse: *Calluna vulgaris*, *Vaccinium myrtillus* in forest (Seiskari 1962; Marcström, Borset and Kraft 1973; Brittas and Engren 1982) changes over time in relation to their light requirements. Hence, to be classified as habitat, both requirements should be satisfied.

Material and methods

The study area was the South boreal forest at Grimsö in Västmanland, Sweden (59°40' N, 15°25' E).

A total of 60 different stands were visited and for each one 5 plots were chosen at random within the stand. The GIS database of Sveaskog enabled us to determine the age for each stand. For the analysis forest stands were grouped in four age classes, in the same way as forestry uses cutting classes:

- CLEARCUTS (0 to 5 years old stands)
- YOUNG FORESTS (6 to 25 years old stands)
- MIDDLE-AGED FORESTS (26 to 75 years old stands)
- OLD FORESTS (more than 76 years old stands)

We studied both the light regime changes with succession and the plant community response to this.

Light regime

We used an empirical method. For each plot, in an imagined cylinder of 10m radius, the vegetation cover was quantified in 4 levels (0-1.3¹m / 1.3-4m / 4-10m / >10m) by estimating the vertical vegetation percentage cover in these 4 levels of the cylinder. This means that we

¹ 1.3m is the standard height for such measurements: human breast height.

looked at the percentage, in each volume, covered with branches, leaves. This method is quite subjective but it enable us to have a general tendency of the lightness through the growing of forest stands.

Stand #	Spot #	Age	0-1.3 m %	1.3-4 m %	4-10 m %	>10 m %
1	1					
	2					
	3					
	4					
	5					

Table 1: Field protocol used on the field to quantify the tree percentage cover.

Ground cover

In the same cylinders the ground cover was characterised with the percentage cover of moss, grass, heather (*Calluna vulgaris*), blueberry (*Vaccinium myrtillus*) and lingonberry (*Vaccinium vitis-idea*). The height of the two main food plants for black grouse, *Calluna v.* and *Vaccinium v.-i.*, were also estimated, as a measurement of the amount of food. Additionally a dense and high field layer can be a better habitat because nesting females can hide more easily in tall vegetation.

Stand #	Spot #	Age	Moss %	Grass %	Calluna vulgaris %	Calluna height cm	Vacc_myrt %	Vacc_myrt height cm	Vacc. vitis-idea %
1	1								
	2								
	3								
	4								
	5								

Table 2: Field protocol to estimate the ground percentage cover.

Results and discussion

Light regime

The first level, 0 to 1.3 meter above the ground, was shaded with a maximum in young forests. It then became more illuminated with the stand age. The same thing occurred between 1.3 and 10 meters, but with a little time lag compared to the first level as it takes some years for the tree to reach that height. In old forests, usually only the trunk was left below 10 meters: the lower branches had died.

The upper level gives a maximum of shade in middle-aged and old forests: 39% (± 19.3). Smaller trees have usually been removed by thinning.

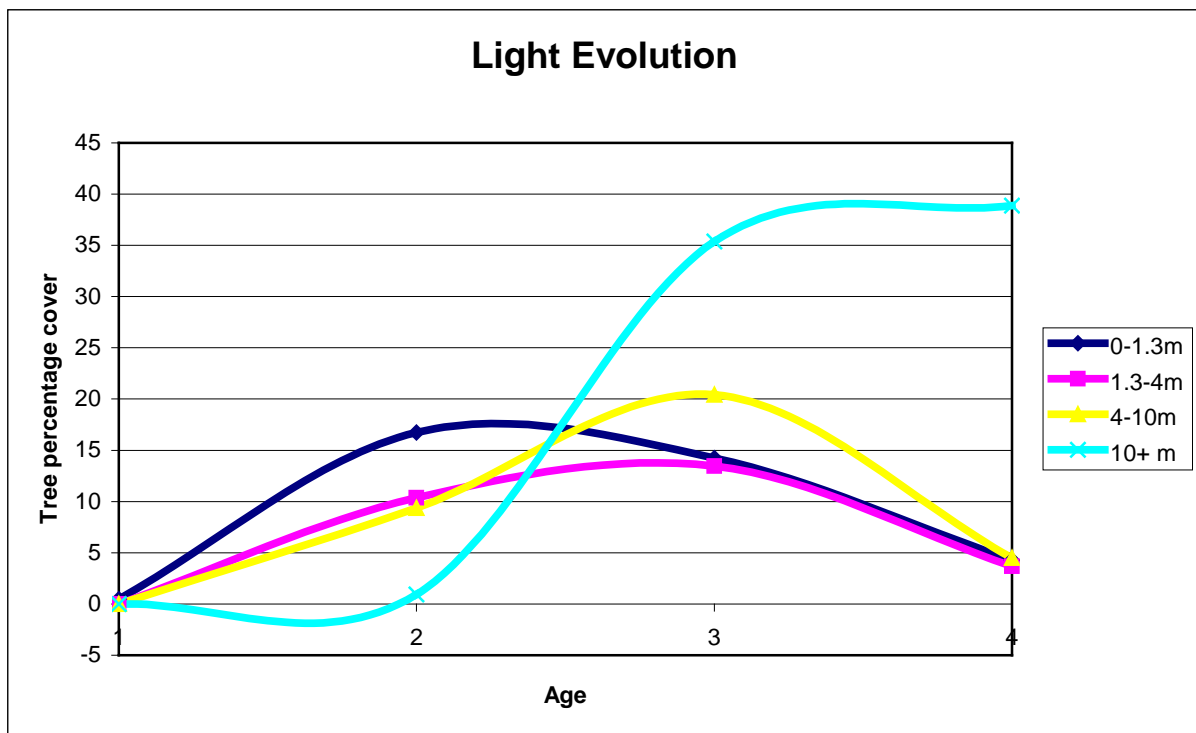
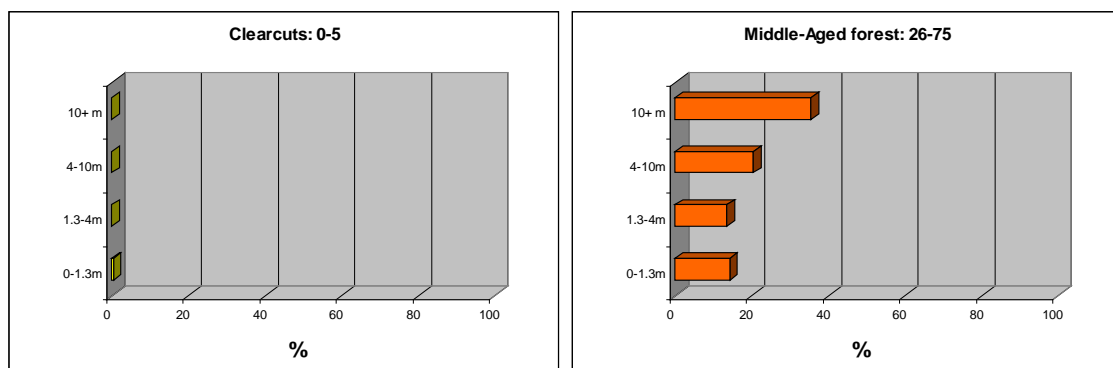


Figure 1: Tree percentage vertical cover at four height levels, in relation with the age of forest. With Age 1 = clearcuts: 0-5 years-old; Age 2 = Young forests: 6-25 y.-old; Age 3 = Middle-aged forests: 26-75 y.-old and Age 4 = Old forests: 75-145 y.-old.

When looking at Figure 2, it appears that after the clearcut, the first trend in the evolution is the covering of the first levels, followed by the upper ones. At the end, the trunks are “naked” and only the canopy is left. But it should be noticed that even with a more important upper cover, old forests are not necessarily more shading than the young ones. This is because the first levels, important in young forests, are making shade on the ground nearly from the sunrise until the sunset. But this might not be the case in old forest: in the morning and evening, only the trunks are shading (see Picture 1). Thus an important difference between the lower and higher level is the number of hours that they really make shade during a day. This is why one cannot use the highest tree percentage cover within the four levels to explain the luminosity on the ground.



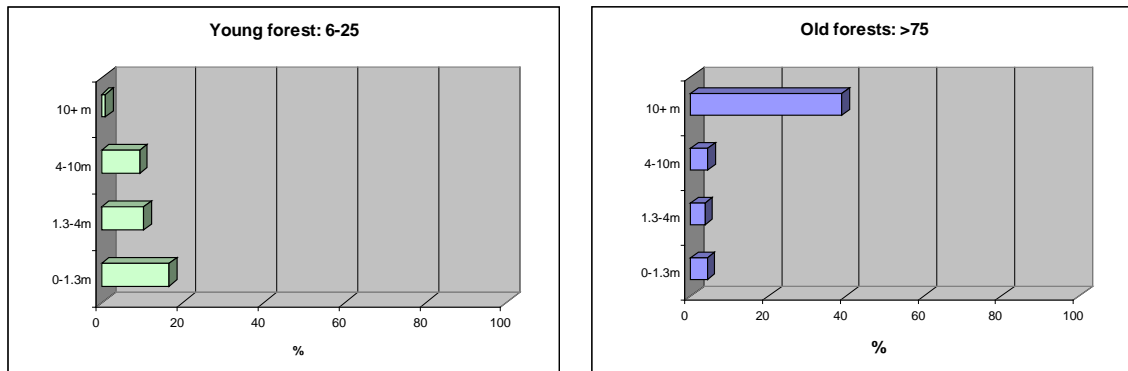


Figure 2: Tree percentage cover at four levels, in each age class.



Figure 3: Difference in the duration of shading in a day between young forests with abundant lower cover and old forests.

Ground cover

Grass are pioneer plants, covering most of the ground in clearcuts. Then they show a sharp decrease throughout the stand age.

Clearcuts constitute a transitional phase: some plants remaining from the old forming forest will still live for a while and plants characteristic of young forests will appear more or less quickly, depending on how much “old forest-plants” were left during the clearcutting (i.e. depending on the competition with those old forest-plants).

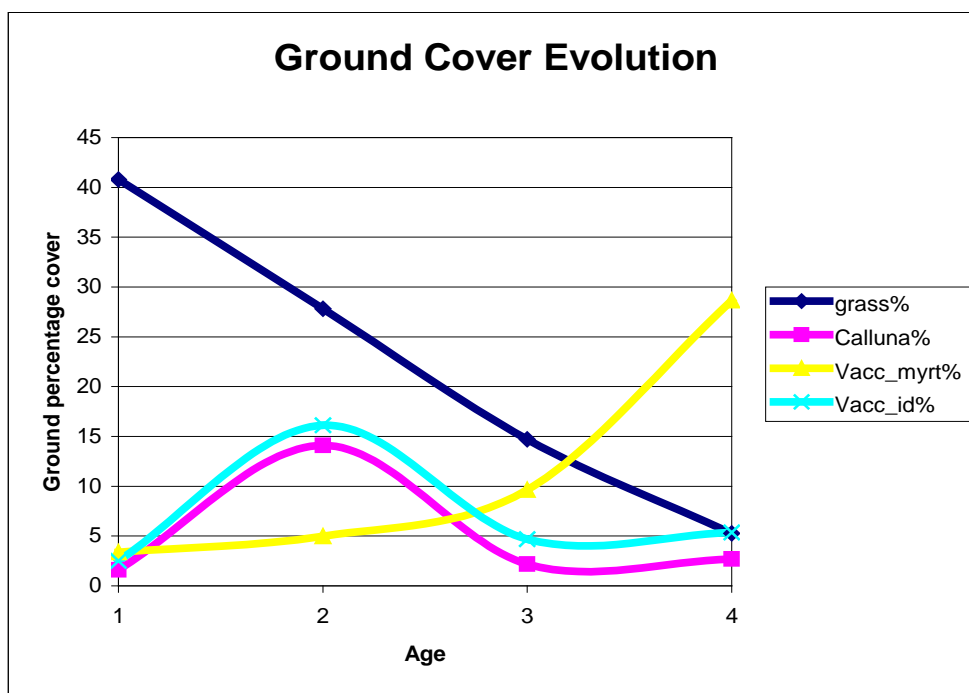
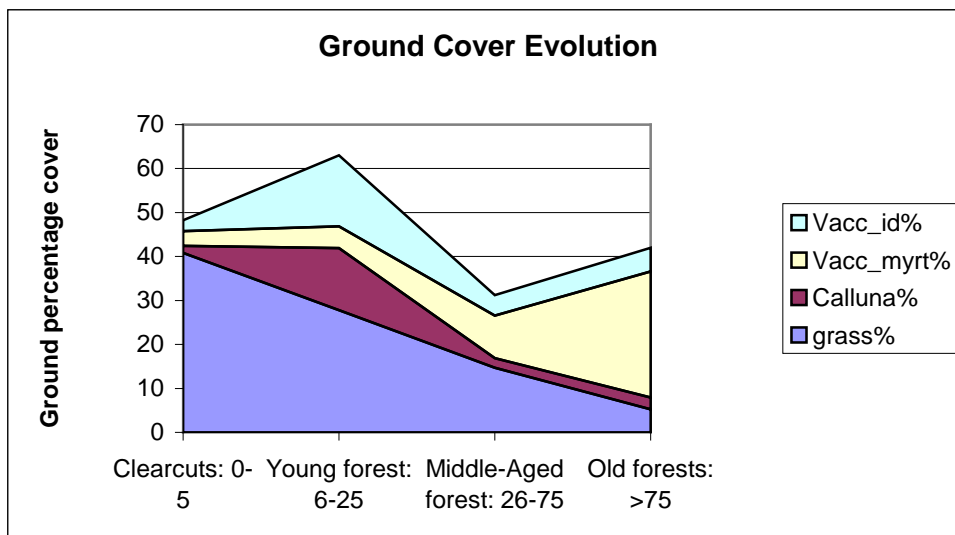


Figure 4 and 5: Ground percentage cover in relation with the age of forest. With Age 1 = clearcuts: 0-5 years-old; Age 2 = Young forests: 6-25 y.-old; Age 3 = Middle-aged forests: 26-75 y.-old and Age 4 = Old forests: 75-145 y.-old.

Amount of food: height measurements

The height of *Calluna vulgaris* does not show any trend over the time (mean = 32 ± 8.1 cm). One can thus not say that their quality is better in young forests than in old ones. *Vaccinium myrtillus* however is taller in old forests (mean in young forests = 15.5 ± 2.9 cm; mean in old forests = 24.3 ± 3.5 cm; the difference is significant according to Fisher's PLSD analyze, with significance level = 5%). But the previous analysis on the ground cover showed us that *Vacc. m.* was probably not an important food plant for black grouse as their presence in the studied forest does not correspond to the "window" used by the bird.

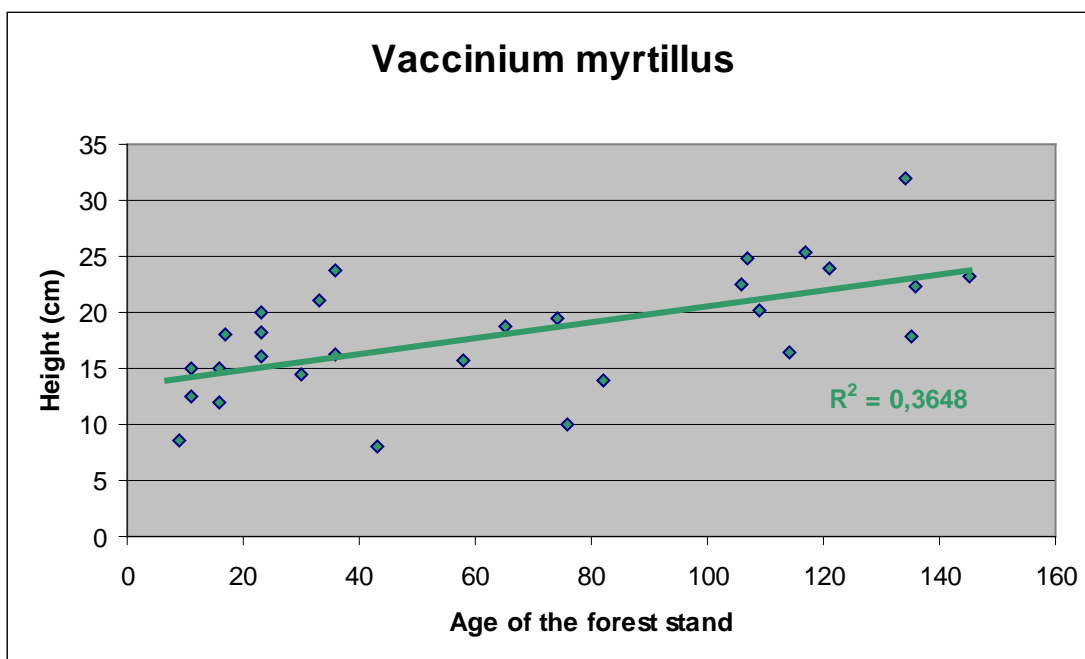
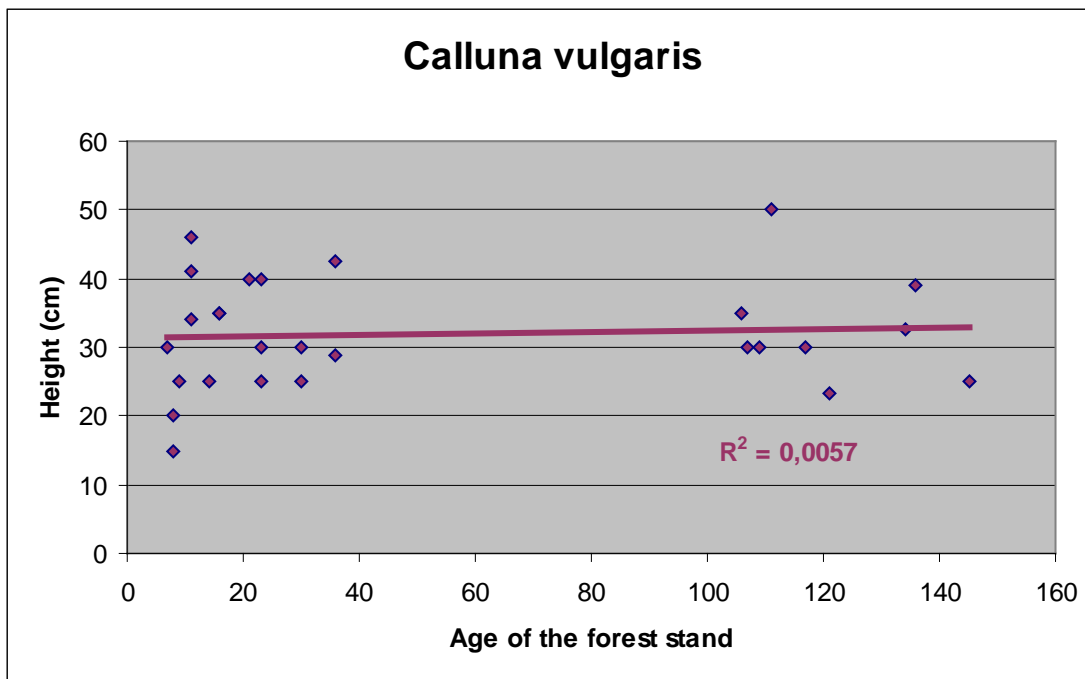


Figure 6 and 7: Evolution of the height (cm) of heather and blueberries with the age of forest stands (correlation coefficient, $r=0.076$, $P\text{-value}=0.71$ for *Calluna v.* and $r=0.60$, $P\text{-value}=0.0004$ for *Vacc.m.*).

Light and Ground correlations

The tendency for grass to decline when forest grows up is confirmed by the correlation analysis. The grass percentage cover was positively correlated to the “0 – 1.3m” level as they are found in young forests. They like light and were thus able to grow in the first years after the clearcut. However, it was negatively correlated to the “>10m” level, which becomes more and more important as forests become older.

Heather (*Calluna vulgaris*) and lingonberries (*Vaccinium vitis-idae*) show the same tendency avoiding forests with an important superior level, i.e. old and middle-aged forests.

Finally, blueberries cover a high proportion of the ground in old forest, with a positive correlation with the “4 – 10m” and “>10m” levels.

	0 – 1.3m	1.3 – 4m	4 – 10m	> 10m
Grass	<u>0.29</u> (0.024)	0.10 (0.45)	-0.12 (0.35)	<u>-0.36</u> (0.004)
Calluna vulgaris	0.12 (0.37)	0.028 (0.83)	-0.12 (0.35)	<u>-0.29</u> (0.022)
Vaccinium myrtillus	-0.24 (0.62)	-0.18 (0.17)	-0.094 (0.48)	<u>0.50</u> (<0.0001)
Vaccinium vitis idae	0.14 (0.29)	0.24 (0.061)	<u>0.31</u> (0.015)	<u>-0.38</u> (0.0028)

Table 1: Correlation coefficients, r, between the ground percentage cover of four field layer plant species and the tree percentage cover; n = 60. The underlined numbers are the significant correlations. P-values are in brackets.

Conclusions

The “window” in time used by black grouse (young forest: 6 to 25 years old) is characterized with:

- a maximum in the vertical cover of low vegetation, but with a mean not exceeding 18% ± 6.06
- a maximum for heather (*Calluna v.*) and lingonberry (*Vaccinium v.-i.*) cover
- a low cover of blueberry (*Vaccinium m.*)

This age class is thus quite luminous, which is favourable to heather. However, blueberry, the other main plant feeding black grouse does not seem to be very important here, in the study area, as it does not exceed 5 % ± 2.3 in young forest and reach his maximum (29 % ± 4.6), in old forests.

Thus the two parameters which have been studied are both required to make stands suitable for black grouse. The habitat, vegetation structure needs to be quite open and the food has to be found.

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Chapter 3 - Effects of 23 years of landscape change on the abundance and lek distribution of black grouse

Introduction

Landscapes are not static in time. Some are very dynamic, such as the boreal forest which is characterised by large-scale stand replacing disturbances. Thus, in such forests, species can be assumed to have adapted to this shifting mosaic of successional stages. To study the effects of the spatial and temporal changes of a habitat on a population, long-term studies are required. To confirm the effect of habitat patch dynamics on black grouse, it was necessary to wait until the whole forest habitat in the landscape had completely changed. Twenty-three years passed since the establishment of the habitat/density model (1979 – 2002). So the forest patches have been spatially re-shuffled.

As a habitat specialist, black grouse tracks the amount of its habitat. When a patch used by a local population becomes unsuitable, this population will go extinct and in places where new good suitable patches are formed, new local populations will appear. This has been confirmed by a comparison of different landscapes at one point time (Angelstam 1983). However, validation is also needed and this is the purpose of this paper. In other words, we want to confirm the spatial trend by looking at a temporal dynamic. In another step for biodiversity purpose, those changes in the occurrence and location of patches can then be used to predict the disappearance of old and appearance of new black grouse leks.

We also expected a gradient North-Middle-South in the study area.

In the south, management units are small as owners are private; patches of young forest never get large enough. The middle and north parts are owned by the National Forestry Company, thus management units are large but big bogs are mainly situated in the middle.

When studying the density of black grouse, one has to count lekking males instead of single ones. This is because of the cyclic density variation which is mainly due to single males (Angelstam 1983). Black grouse show a cyclic dynamics (3-4 years), in relation with vole density. It is the “alternative prey hypothesis”: when voles are at their lower density, their predator, foxes, switch their diet onto black grouse. Thus single males are not really useful for such studies, making it much more difficult to interpret.

Material and methods

The study area: the transect

The study area was situated in Västmanland, Sweden. This place has not been chosen at random: studies on population dynamics should be made where the population is still “healthy”, not where it is close to extinction. The Grimsö Wildlife Research Area was covered with a grid of 36 plots, 4x4 km each (= 48x12 km, i.e. 576 sq. km).

Habitat and biology

The black grouse is a lekking bird. A group of cocks displaying collectively on open areas with the aim of attracting females for mating. When a new lek is created, cocks attend it throughout the year, with two main periods of activity (the most intensive one is in spring, March-May and the secondary one is in autumn, late August-October) and with the exception

of two months in midsummer when males moult (Baines 1994). This is why, unless habitats change, leks tend to persist from year to year with little or no change in location. The one year-old males are usually solitary as they are not yet integrated in a lek. However, if the population density is low, also older males may display solitarily.

Black grouse is looking for an open landscape, between forest and bogs. This is because of its biology and behaviour. It needs a dense cover on the ground to nest, feed and hide from predators; scattered trees to perch and watch; open spaces to gather and display: bogs, old cultural landscapes, field and clear-cuts (Ruwet et al. 1997).

Black grouse habitat

In the boreal landscape, black grouse are found in three types of habitats.

- Old cultural landscapes: In the 19th by black grouse inhabited this type of landscape, with open fields, heathlands and pasturelands, which were surrounded by forests (Ekström 1894). But nowadays, those are all gone in the study area, being replaced by intensive farming (tree plantation on heaths, disappearance of woodland pastures and wooded meadows, autumn ploughing,...).
- Open bogs: Among several types of bogs and mires, the open sparsely vegetated ones are the preferred ones (Byrejedal et al. 1997). If not affected by human (as it is the case in Western Europe), bogs are spatially quite stable over the time.
- Young forest: Black grouse use a “window” in time in the successional stages in forest, between 5 and 25 years after the logging (Seiskari 1962). This type of landscape used to appear after large scale disturbances (fire, storm, avalanche). It resulted in a patchy distribution of different successional stages within the forest (Heinselman 1981). Nowadays, such disturbances are very rare; however forestry tends to “replace” the natural process, providing young forests after clear-cutting (Gamlin 1988). Both today’s commercial forests and the primeval forests thus can be characterised as a mosaic of stands, although today’s stands seem to be considerably smaller (Rowe 1979, Andersson and Hultman 1980). This type of landscape is very dynamic: as years are going on, patches of young forest are “re-shuffled”. Boreal forest species, therefore, provide a good opportunity to study if and how patchiness affects animal densities.

Characteristics of the transect

Regarding to the landscape, the 576 sq. km transect could be divide in three parts: the North, the Middle and the South. In the South, old cultural landscapes are gone. They were previously suitable habitats for black grouse. This area is the most inhabited, with a lot of intensive farming. Forest is owned by private landowners, this means that patches are quite small. The Middle is characterised by big bogs. In the North, bogs are small but the forest is quite important. Both Middle and North forest is owned by Forest Company; patches are thus bigger compared to the South area.

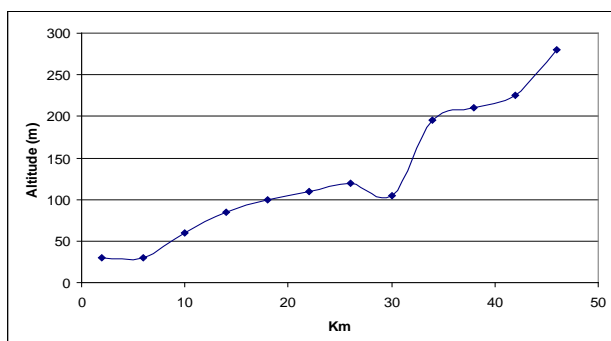
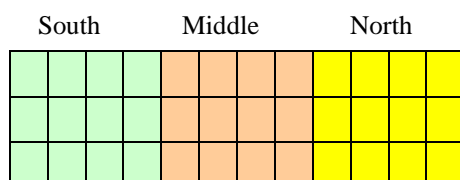


Figure 1: The study area and the transect.

Counts of black grouse

Counts of black grouse were repeated, in the same way as the previous study in 1979. The first part of the work consisted in locating single males and leks. This mean that all squares

were covered by car in a way that two stops weren't distant more than 1.5km, as black grouse can be heard at a maximum distance of about 800 m, in good weather conditions (Angelstam 1983).

In a second time, all leks were visited to count the cocks. All counts were conducted in April, from the sunrise 3 hours after sunrise, i.e. when the displaying spring activity is at his peak (Hjorth 1970). Data were then compared with 1979 results.

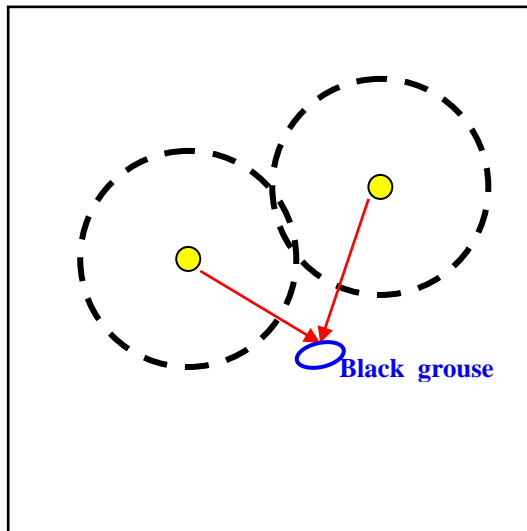


Figure 2: How to spot black grouse? On each stop, yellow points, a bearing is taken: the direction in which the bird is heard. Black grouse is then spot at the point where 2 arrows join each of them. The black circles represent the area in which birds are audible, when stopping in their middle.

Results

The whole transect

The number of leks and lekking birds in the whole transect did not change significantly from 1979 to 2002 (see Appendix 1 for the detailed results). Only the number of solitaires is quite higher in 2002 but this may be due to the cyclic dynamic in relation to the vole density.

	1979	2002
Number of leks	24	28
Lekking cocks	192	177
Solitary cocks	69	117
Total number of cocks	261	294

Table 1: Results from the total counts.

When looking at the mean number of cocks on leks for the whole transect (table 2) there was no significant difference between the two years of study (Anova and Fisher's PLSD analyse: Mean-diff. = 0.518, Crit. Diff. = 2.822, P-value = 0.714).

	1979	2002	P-Value
No. of cocks/lek	7.37 ±1.1	6.86 ±0.92	0.714

Table 2: Mean of the number of cocks on each lek, in 1979 and 2002; whole transect.

The three parts in the transect

The table 3 is a summary of all counts from both 1979 and 2002 for the three parts of the transect. No leks were found in the South in 1979 and only one in 2002. Most of the leks were found in the Middle and the North. However, solitary cocks were found in the whole transect, even in the South.

Part of the transect	Leks no.		Lekking cocks		Solitary cocks	
	1979	2002	1979	2002	1979	2002
North	10	10	57	56	53	22
Middle	14	17	120	132	37	36
South	0	1	0	4	27	11

Table 3: Summary of the results from the counts of black grouse in 1979 and 2002, in the three areas of the transect.

See map resuming the distribution of leks in 1979 and 2002 in the studied transect.

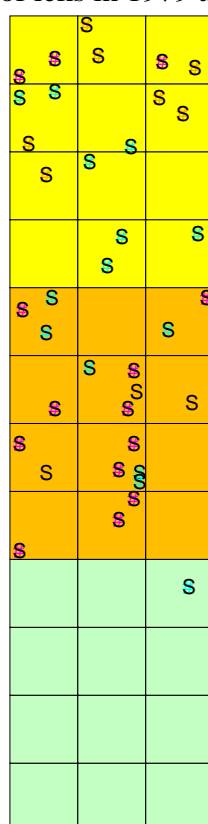


Figure 3: Distribution of leks in the transect. Legend: Yellow squares = North, Orange = Middle and Green = South. Orange dots represent leks from 1979 only, Blue dots = leks from 2002 only and Pink dots = from both 1979 and 2002.

No significant differences in the mean number of males per lek was observed in the three parts of the transect (Anova and Fisher's PLSD), see Tables 4 and 5:

- nor between the mean for each area in 1979 / 2002 (ex: North_1979 and North_2002)
- nor between North / Middle / South in the same year (ex: North_1979 and Middle_1979)

Part of the transect	1979	2002	P-Value
North	5.70 ±1.03	5.60 ±1.02	0.96
Middle	8.57 ±1.6	7.76 ±1.4	0,66
South	-	4	-

Table 4: Mean of the number of cocks on each lek, in 1979 and 2002, for the three areas of the transect.

	P-Value
North 1979 – Middle 1979	0.17
North 1979 – South 1979	-
Middle 1979 – South 1979	-
North 2002 – Middle 2002	0.29
North 2002 – South 2002	0.76
Middle 2002 – South 2002	0.47

Table 5: P-Values of the Fisher's PLSD analyse, comparing the number of lekking cocks between the tree areas. Significance level = 5%. As no leks were found in the South in 1979, there is no P-Value.

Dynamic of leks in the transect

Proportion of leks

A good way of looking at the dynamic or stability of leks within the transect is to analyse their proportion in the three areas. The South part should not be taken in account as it is only represented by one lek. On the other hand, the difference between the North and the Middle is quite clear. In the North, only a few leks were located in the same place in 1979 and 2002. In the Middle however, most of the leks still were at the same place as in 1979. In this part of the transect, black grouse were thus more stable.

	1979	2002	1979 & 2002	Total
North	7	7	3	17
Middle	3	6	11	20
South	0	1	0	1

Table 6: Number of leks.

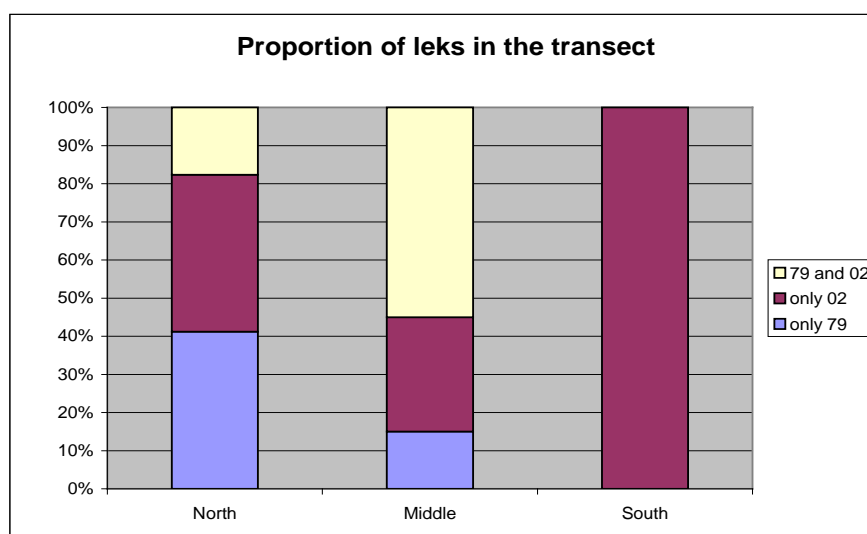


Figure 4: Porportion of leks observed in 1979, 2002 or both years, for each area of the transect.

Correlations: number of leks, lekking and solitary birds.

The relationship between the number of leks in each sampling square in 1979 and 2002 was significant in the Middle part of the transect but not in the Northern part. In the South there were no leks in 1979 so no correlation can be established (cf. Table 7 and Appendix 2). The same results are found for the number of lekking cocks in each sampling square.

Solitary birds, however show no significant correlation in the North and the Middle of the transect but well in the South (Table 7).

Part of the transect	Number of leks	Lekking cocks	Solitary cocks
Whole transect	0.58 (0.0002)	0.72 (<0.0001)	0.12 (0.49)
North	-0.04 (0.91)	0.26 (0.43)	-0.03 (0.92)
Middle	0.71 (0.0071)	0.73 (0.0053)	-0.17 (0.61)
South	-	-	-0.80 (0.0009)

Table 7: Correlation coefficients, r , between 1979 and 2002 ($n=36$ for the whole transect; $n=12$ for the three areas): number of leks, of lekking cocks and of solitary in each sampling square. Significant coefficients (significance level = 5%) are marked underlined. P-values are in brackets.

Part of the transect	Leks	Solitary
Whole transect	<u>0.49</u> (0.002)	0.26 (0.13)
North	-0.17 (0.61)	-
Middle	<u>0.82</u> (0.0006)	-0.21 (0.52)
South	-	0.51 (0.094)

Table 8: Correlation coefficients, r , between 1979 and 2002 ($n=36$ for the whole transect, $n=12$ for the three areas): presence/absence of leks and solitary males in each sampling square. Significant coefficients (significance level = 5%) are marked underlined.

Discussion

Landscape type and black grouse dynamics

The difference in the dynamics and stability of leks among landscape type was confirmed by the comparison in the location of leks in 1979 and 2002 proportion and by the correlation analyses among the sampling squares.

The North, with few “both years” leks, showed no correlations between the counts in 1979 and 2002; nor in the number of leks, nor in the number of lekking birds in each sampling square. This is consistent with the hypothesis that leks have been re-shuffled in the same way as young forest patches have. The Middle part of the transect, with many stable leks, we found a positive correlation in the number of leks and in the number of lekking birds among the 12 sampling squares. This means that most of the leks are still at the same place as in 1979. In the South no spatial or temporal changes could be made as only one lek was found.

Solitary cocks showed no correlation in their distribution between 1979 and 2002 in the North and Middle part of the transect. This is because solitary cocks are usually young males (1 or 2 years-old), which have not been able yet to enter a formed lek. Consequently, they cannot be used to show the dynamic or stability of leks. First, because their minimum required area

(0.20 sq. km) is quite inferior than for a lek (0.90 sq. km, Angelstam 1983). And second, they are not territorial and move around from one suitable area to another.

The South is an exception: solitary males show a correlation in their distribution over the time. The suggested explanation is that here, even if solitary, males are probably older than “usual” solitaires. They can then be territorial and stay at the same place over the years. As suitable patches for black grouse are not numerous in the South, the same ones tend to be used, by successive males.

Leks sites and habitat patches

The North part of the transect, with spatially dynamic populations of black grouse is characterised by small bogs with a lot of forest. The Middle part has many big bogs and stable populations (ex: Spelmossen, Orrmossen, cf Appendix 1). The difference in stability between those two areas is explained by the minimum area requirement and the difference between the lek site and the habitat. The minimum area requirement for a lek is 0,90 sq. km (Angelstam 1983).

In the Middle several bogs are big enough to fill the area requirement of black grouse. The absence of successional development makes them a stable habitat over time. However in the North of the transect bogs are only big enough to be lek sites but not the whole habitat which is also composed of young forests. As forests are very dynamic in time, patches of young forest “move” from one place to another (at the rhythm of clear cutting). A place which was a good habitat at one time will soon become unsuitable. Black grouse follow this dynamic by moving to bogs newly surrounded by young forest. The case of the South part is quite different: here there are no bogs, no old cultural landscapes anymore (which were previously suitable habitat, in the 19th) and the forest owners are privates thus patches are too small to fill the habitat requirement for black grouse leks.

From a management point of view, this means that protecting lekking areas is not sufficient: protective measures should be extended to areas used for feeding, resting, nesting purposes as well, i.e. the entire vital zone (Bouvier 1989).

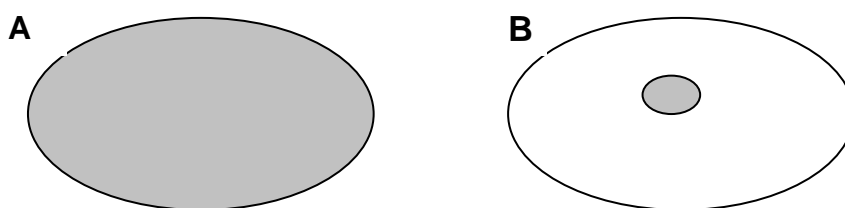


Figure 5: The habitat is represented in white and the lek site in grey. The picture A represent the case of the Middle part of the transect: bogs are big enough to be leks at the same time as habitat. The picture B represent the North part of the transect where leks are only a little area in the whole habitat.

Conclusion

The aim of this study was to test the hypothesis that black grouse track the amount of their preferred habitat. As an area-demanding species and a potential umbrella species, it has to represent a type of landscape. We saw that those birds really follow the amount of their suitable habitats. If their habitats are “moving”, as in the North part of the transect, it will be

reflected on the distribution of leks. When a place become unsuitable as a black grouse habitat, the lek will disappear and new leks will be formed in new good patches. If their habitats are stable in time, as in the Middle part of the transect, leks will not change spatially, remaining in those good patches. Thus due to their complex demands on the habitat (e.g. spatial and temporal configuration of habitats), their close relationship to habitat, black grouse indicate specific requisite of a habitat by their appearance. They react to both natural or man-made changes in their specific habitat by population increase or decrease.

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Discussion – the work in an European context

Black grouse populations in central Europe are known to fluctuate more or less periodically, with, generally, a superposed decline of the numbers of birds (Loneux and Ruwet 1997). But according to its extended distribution, the black grouse is not a globally threatened species. The causes of this decline are really numerous and not general: every country, every population has its own main problem. This has been pointed out with the results of a questionnaire sent in 29 countries within the range of black grouse (Europe and Asia), cf. Storch 2000. The same appears when comparing different population evolutions: there are no general trends, which confirms that each local population has to be taken as a single case. However, the habitat degradation is generally the most implicated factor in the decline of black grouse population (Loneux and Ruwet 1997).

To put the results in a European context, I discuss the similarities and differences between the long-term black grouse study, and the trends in other local black grouse populations in Europe.

Type of dynamics	Section of the transect in this study	European examples
Dynamic	North: boreal forest	Restoration of forest on moorland in Scotland and Wales
Stable	Middle: raised bogs	Lowland central Europe
Declining	South: former cultural landscape	Cultural landscapes in both lowlands (Rhön, N Austria) and the Alps

Dynamic landscape: Scotland, Britain and Wales (United-Kingdom)

Forests are here the natural landscape. But with the human action, it had changed into open moorlands. However in the last decades, managed areas tend to be reforested. In Britain, black grouse occur on the edge of native woodlands, either pine or birch (Picozzi and Hepburn 1985), or along the edges between heather moorland and rough grazing pastures and meadows (Baines 1994). Temporally changing habitats are provided by afforestation of moorland. Black grouse rapidly colonise areas with newly planted trees but their number decline rapidly as the trees mature when the forest canopy closes.

In the Scottish moors there is a dynamic equilibrium between areas supporting high densities of herbivores and areas with more extended grazing. In the first one the management consists in fire to promote the growth of the vegetation. The second one provides open landscapes but still with a tree cover. To ensure the maintenance of black grouse, it is necessary to manage moors in an equilibrated way: overgrazing and excessive fires may destroy the habitat (Moss 1989).

Stable habitat: Hautes-Fagnes (Belgium) and Upper Swabia (Germany)

The Hautes-Fagnes is a national reserve since 1957. The reserve was created to safeguard open landscapes with moors, heathlands and the associated fauna (Ruwet et al. 1997).

Until the middle of the 19th, extensive farming was practiced. But between 1850 and the 1960's, poor landscapes were exploited, mires and bogs were drained, spruces were planted.

The landscape became more and more close. When looking at the population evolution since 1966 black grouse showed a peak from 1967 to 1972 (with a maximum of 198 males). Since then the population is quite stable but still at the limit of extinction (between 30 and 60 males): bad conditions can easily lead the bird to disappear from this area. (cf. Appendix 4)

In Upper Swabia, Germany, the autochthonous black grouse population was extinct (cf. Appendix 5). Before introducing new birds, the losses and changes in habitats, as possible causes of extinction, were quantified. The peat exploitation was intensified in the early 20th. Litter meadows were transformed in intensely grazed meadows. The drained and peat cutted areas developed into heath and dwarf shrubs heath. Then, in the middle of the 20th, draining and peat cutting became intermittent thus pristine rain bog areas could be preserved to a large extent. The decline in the larger bogs proved not to be due to changes and losses of habitats in contrast to the small bogs. In big bogs the main cause of decline was probably the impact of predators from the surrounding areas into the habitat islands, as a consequence of the edge effects (Strauß et al. 2000).

Comparing those areas to the transect, we can say we are in the Middle case. Bogs are maintained open by human and this gives a stable habitat, even if for the long-term survival of the population the protected and managed area should quite more important. As in the middle, a stable habitat is reflected by a stable population.

Old cultural landscape: Rhön (Germany), Alps, Denmark

The black grouse population of the Rhön lives in an ancient and open cultural landscape. The actual core-area in this low mountain area is the nature reserve “Lange Rhön”², where a small isolated population has survived until now (Kolb 2000). The situation of the population is critical. It reached a minimum of 12 cocks and 5 hens in 1996. With the recent management of the area the population size was 27 cocks and 16 hens in 2001 (cf. Appendix 6).

During centuries, the extensive land use by grazing and/or mowing giving those typical mountain meadows (with single bushes, small groups of trees as well as low moors and bogs). But farming is more and more in retreat and as a consequence, natural succession takes place and simultaneously with the spread of shrubs, bushes and, later on, trees, important habitats of black grouse and other birds of open landscapes get lost. Thus, the conservation of this type of landscape requires management. In this reserve several steps in conservation have been conducted since the beginning of the 1980's (mowing, removal of scrubs and spruces). For example, due to the action of wood reduction in 1997, the sample area becomes again attractive and useable for species of open landscapes such as black grouse (Kolb 2000).

Comparing to the transect in Grimsö, we are in the same situation as in the South area: black grouse disappear in the same time as the previous old cultural landscape. In the Rhön reserve black grouse is a flagship species. Variations in its population indicate where changes in the landscape occurred and thus where management is required. The subsequent variation in its density enable to judge of the pertinence of the management.

The Alps situation is the same. Too important reductions of the vegetation cover, by overgrazing, is negative to black grouse. However opening landscapes is beneficial. In the Alps, the abandon of the pastoral activity, was benefic in a first time, but then promoted the

² Designated as a nature reserve in 1982, with a size of 2657 ha.

closing of the landscape. The population has been declining in the last years (cf. Appendix 7). And to favour black grouse, it is needed to reduce the progression of spruces and alders.

To conclude, it is important to compare different landscapes to understand the factors affecting the distribution and abundance of black grouse.

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Appendix 1a: Table with all leks in the transect. Legend: Year 7902 = leks present in both 1979 and 2002.
Lek_1979 and Lek_2002 = number of cocks attending each lek.

ID (4x4)	ID (1x1)	NAME OF THE LEK	YEAR	LEK_1979	LEK_2002
1	11	Sångarbergsmossen	7902	14	4
1	13	Övre Sandtjärn	7902	6	4
2	1	Getmossen	1979	4	0
2	10	500m NV Gölmosse	1979	4	0
3	10	Morasmossen	7902	8	12
3	14	SE Övertjärnen	1979	5	0
4	3	Rackarmossen	2002	0	5
4	13	Clearcut 1500 m SW Sandtjärn	1979	5	0
4	1	Storstensmossen	2002	0	3
5	16	NW Lien	2002	0	3
6	2	300m NW Knutsmossen	1979	5	0
6	7	Övre Skärsjön	1979	3	0
7	7	Clearcut SW Bäcke-gruvan	1979	3	0
8	2	Hästmosse	2002	0	8
11	3	Dammossen	2002	0	10
11	14	Glifsmossen	2002	0	3
12	4	E Forsen	2002	0	4
13	3	Fänsäter field	2002	0	14
13	5	Gäddtjärns-mossen	7902	4	3
13	14	Källmosse	2002	0	8
15	4	Ormosse	7902	22	20
15	10	Dagkarls-mossen	2002	0	7
16	15	Kringelmossen	7902	13	5
17	1	Åkerhed	2002	0	4
17	4	Stormossen	7902	8	8
17	8	S Stormossen	1979	3	0
17	15	Spelmossen	7902	19	20
18	11	Tjärnmossen	1979	3	0
19	1	Stenkärsmossen	7902	8	6
19	14	LjusÖsarna	1979	7	0
20	11	Gäls-mossen	7902	3	2
20	8	Snärmosse	7902	6	5
20	16	Gubbmossen North	2002	0	3
20	16	Gubbmossen East	2002	0	3
22	13	Mattabromossen	7902	5	11
23	4	N Svartjörms-mossen	7902	14	10
23	7	V Svartjörms-mossen	7902	5	3
27	7	Lapptjärns-mossen	2002	0	4

Appendix 1b: Identification numbers (ID) of each 4x4 and 1x1 km square in the grid.

1	2	3	4	2	3
5	6	7	8		
9	10	11	12		
13	14	15	16		
4				5	6
7				8	9
10				11	12
13				14	15
16				17	18
19				20	21
22				23	24
25				26	27
28				29	30
31				32	33
34				35	36

Appendix 2: Graphs of the correlations between 1979 and 2002 for the number of leks, lekking males and solitary males.

